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FLORAL MORPHOLOGY IN RELATION TO POLLINATION ECOLOGY IN FIVE QUEENSLAND COASTAL PLANTS

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Abstract.

Observations of pollination by birds in *Acanthus ilicifolius* and *Lysiana subfalcata* var. *maritima*, hawkmoths in *Clerodendrum inerme* and *Sonneratia alba*, and bees in *Sesuvium portulacastrum*, are presented along wth detailed descriptions of floral morphology and pollination efficiency using pollen/ovule ratios. Self-fertilization is restricted in *Sesuvium, Acanthus,* and *Clerodendrum* by protandry, while the flowers of *Lysiana, Sonneratia,* and *Acanthus* are morphologically incapable of automatic self-pollination. The high fruit set seen in flowers of these species suggests that these species are self-compatible. Self-compatibility in mangrove and mangrove-associated species will presumably allow some fruit set even in isolated, single plants after a new habitat is colonized.

Information on the reproductive biology of plants forming or often associated with mangrove communities has generally been limited to the fruit dispersal stage (see Guppy, 1906; Rabinowitz, 1978). Recent studies in Australia have shown an extensive array of floral adaptations in relation to different pollinator visitors and plant-animal interrelationships in the genus *Lumnitzera,* Combretaceae (Tomlinson *et al.,* 1979) and the tribe Rhizophoreae of the family Rhizophoraceae (Primack and Tomlinson, 1978; Tomlinson *et al.,* 1979). The present study reports on the floral morphology, pollination ecology, and fruit set of five species found in the mangrove or other coastal vegetation of northern Queensland. This information provides a better understanding of the dynamic interactions among plants and animals in and near the mangrove forest.

MATERIALS AND METHODS

Observations were made at Cape Ferguson, near Townsville, Queensland (19°4'S, 147° 17'E) during March and April 1978. The methods for determining pollen/ovule ratios and stigma receptivity have been described by Tomlinson *et al.* (1979). To summarize, the number of pollen grains per flower was determined either by direct count of macerated anthers or with a Coulter Counter, and of ovules by direct dissection. The onset of stigma receptivity was determined by floating stigmas in (a) α-naphthyl acetate, and observing a color reaction at the stigma surface, indicative of esterase activity by a coupling with (b) hexazotised pararosanilin.

Descriptions of floral characters directly related to pollination were made using fresh material, but the illustrations were prepared from fluid-preserved material. All information on flower phenologies and pollinator visits were made on natural populations. Collections were made of insect visitors to these flowers; these insects were identified by members of the C.S.I.R.O. Division of Entomology, Canberra. Fruit set was determined for three species by tagging either flower buds about to open or open flowers in April 1978, and returning two weeks later to check for developing fruit. Information on the growth habit, typical habitat, and geographical distribution of each species is presented in Table 2.

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SONNERATIA ALBA J. SM. (SONNERATIACEAE)

This is a tree of the seaward community of mangroves with the flowers conspicuous and terminal on the ultimate branches (Fig. 12). Each flower has approximately 300 stamens which form the attractive part of the flower; each stamen is about 25 mm long. Some of the stamens point outward, while others are angled inward, forming a network of filaments about 30 mm in length over the ovary (Fig. 12D). The stamens are partially supported by the five thick, green calyx lobes, which are often purple at the base. The style extends beyond the anthers, then bends upward, and ends in a sticky, disc-shaped stigma. Automatic self-pollination is minimized because the stigma extends beyond the anthers. Many drops of nectar accumulate along the margin of the ovary.

The flowers last only one night, they open at dusk or just after dusk and are often orientated towards the setting sun. The following morning the stamens fall off and the stigma discolors. About one hour after the flower opens, a sour-milk odor is produced and the anthers begin to dehisce. The light, powdery pollen is produced in very large quantities (500,000 grains per flower). Bees sometimes land on the opening flowers but are generally unable to penetrate the tangle of filaments and do not contact the stigma.

Hawkmoths were observed visiting the flowers, and appear to be the primary pollinators in this area. Alighting for only a few seconds on a flower before resuming flight, moth activity was relatively low. Individual flowers probably were visited no more than twice during the two hours over which observations were made; however, this is presumably sufficient for pollen transfer to take place. Two hawkmoths of the same species *(Psilogramma menephron menephron* [Cramer])were captured, averaging 1.3 g in weight, and 88, 87 and 56 mm for proboscis length, wing-span, and body length respectively. A proboscis of this length would allow the hawkmoth to take nectar from a distance.

Of 46 flower buds tagged in this species, forty-one developed into young fruit; fruit set was 89%.

CLERODENDRUM INERME GAERTN. (VERBENACEAE)

This is a sprawling shrub of mangrove margins with white flowers in corymbose cymes, with the two to eight flowers in each cyme held horizontally in a single plane (Fig. 13). The corolla has five reflexed lobes and a tube 30 mm long, 15 mm wide at the opening, and 1.4 mm wide at the base. On the inner surface, the corolla tube is densely covered with short fine hairs, presumably to keep out unwanted flower visitors. The calyx forms a cup which extends above the ovary and is covered with an irregular series of raised elliptical glands which apparently function as extra-floral nectaries, since ants are commonly observed feeding at them. Four stamens extend 30 mm from the corolla mouth when the flower first opens (Fig. 13A). The included part of the filaments is white, the excluded part is purple. Each versatile anther sac splits longitudinally in the middle, exposing the thick yellow back of the anther and pulling pollen into a groove formed between the split anther edge and the back of the anther. After the first day and night, the stamens wither away and the filaments roll up. The style is only about 30 mm in length at anthesis, increasing to 60 mm by the second or third day, when the two stigma lobes diverge and the flower becomes receptive to pollen (Figs. 13B, C). These flowers are therefore strongly protandrous, with limited chance of pollen being transferred from anther to stigma within the same flower. Further, all flowers in a single inflorescence generally remain at the same developmental stage, so that flowers on the same inflorescence are unlikely to pollinate each other, though inflorescences at different developmental stages are often

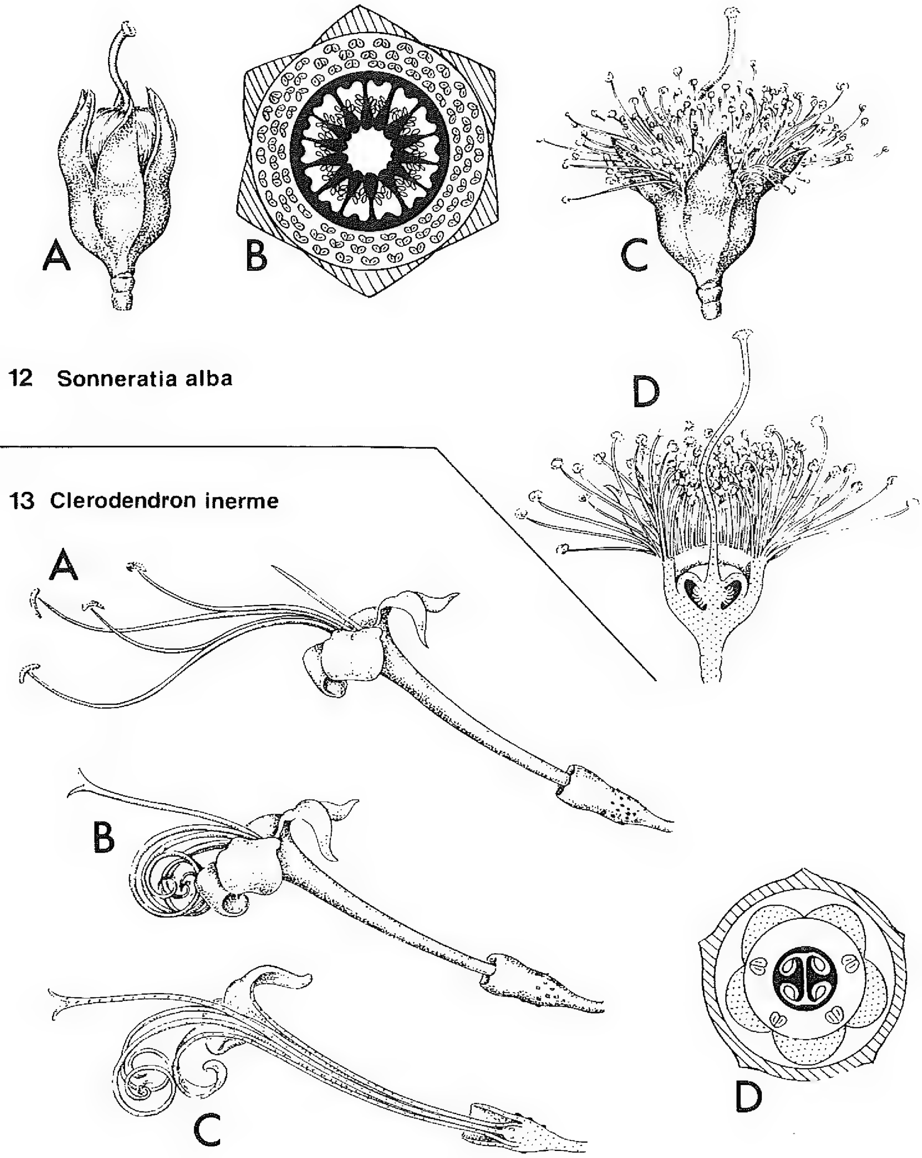


Figure 12. *Sonneratia alba* J. Sm. (from fluid-preserved material, Cape Ferguson, Townsville, Queensland). **A.** Opening flower bud (x 2/3). **B.** Floral diagram. **C.** Open flower (x 2/3) at anthesis from the side. **D.** Open flower (x 2/3) in longitudinal section.

Figure 13. *Clerodendrum inerme* Gaertn. (from fluid-preserved material, Cape Ferguson, Townsville, Queensland). **A.** Flower (x 2) at anthesis (male phase) from the side. **B.** Flower (x 2) at female phase from the side. **C.** Flower (x 2) at female phase in longitudinal section. **D.** Floral diagram.

found on the same plant. The stigma of a single flower may be receptive from one to several days,with individual flowers lasting three to five days.

The flowers are very fragrant. No daytime visitors to the flowers were observed in several hours of observation. In two hours of observation at and just after dusk, one large hawkmoth was the only flower visitor to a large flowering bush. The hawkmoth appeared and departed suddenly. In this brief visit, the hawkmoth probed virtually every flower on the bush, spending only a second or two on each flower.

Adaptations for hawkmoth pollination appear to be the long corolla with hairy interior to exclude other insects. The white corolla and strong fragrance presumably aid the hawkmoths to locate the flowers. The versatile anthers with pollen in grooves, allows the pollen to be placed precisely on the hawkmoth proboscis. The purple color of the filament and style presumably make them difficult for the hawkmoth to see and avoid. No data was obtained on fruit set.

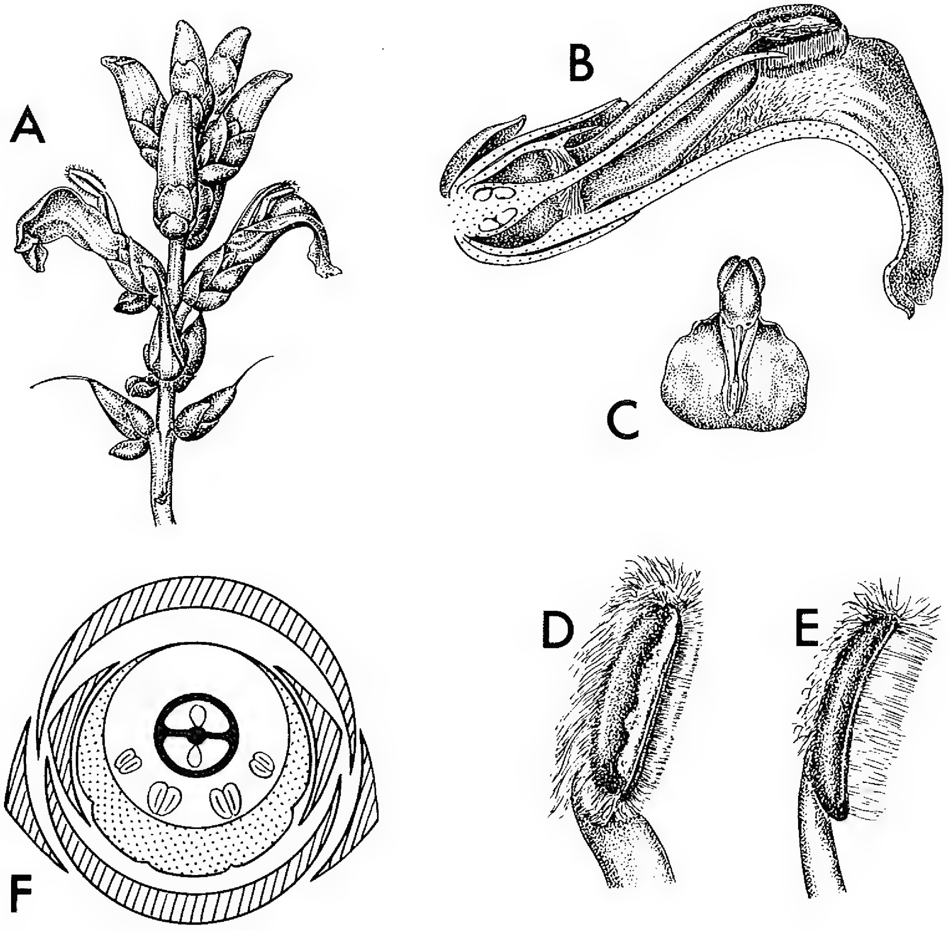
ACANTHUS ILICIFOLIUS L. (ACANTHACEAE)

Acanthus ilicifolius is a shrub or sprawling woody herb with conspicuous blue flowers borne in terminal spikes (Fig. 14A). The corolla is divided into two small upper lobes, and one large recurved lower lip some 35 mm broad and 27 mm long (Fig. 14B, C). The four stamens are in two slightly unequal pairs with their anthers pressed together under tension facing the lower lobe. The anthers (Fig. 14D, E) dehisce longitudinally, with a thick line of hairs lining the split so that pollen is presented on the lower side of the stamens. The stigma rests on top of the anthers, but is prevented by the hairs from coming near the pollen. There is a ring of dense hairs at the base of the stamens where the floral tube narrows (Fig. 14B). All of these hairs point upward and outward, preventing insects from crawling into the floral tube.

A large pollinator visiting the flower probes into the channel about 12 mm long, formed between the stamens and the large corolla lobe below. When the bases of the stamens are touched by the pollinator, they readily diverge in pairs and the style and stigma descend. When pressure on the stamen bases is released, the stigma lifts up and the stamens come back together again. The result is that the stigma touches the back of a pollinator first and picks up pollen, and pollen is deposited by the flower as the pollinator withdraws and the stamens come together again. As a result of this functional morphology, the stigma and the dehisced anthers rarely contact one another. Self-pollination can occur if the stigma does not return to its original position sufficiently rapidly.

The stigma has two lobes which diverge slightly. On the basis of stigma staining, the stigma does not appear to become receptive until the second day the flower is open. The flowers usually last two days, with exceptional flowers lasting either one or three to four days. Pollen was present in the anthers of all flowers examined, regardless of their age. While the flower morphology tends to prevent the self-pollination of a flower, self-pollination is further restricted by the weak protandry. When pollinator activity is high, all the pollen could be removed from the anthers before the stigma becomes receptive.

The only pollinator seen on a patch of approximately one hundred flowers during six hours of observation was a yellow-breasted sunbird (*Nectarina jungularis*) which perched on the stems and probed in most of the flowers. *Xylocopa* bees, which are also suspected of being pollinators, were seen in the vicinity but did not visit these flowers. The pressure which must be exerted on the stamen bases for them to separate and the distance of the anthers and the stigma from the nectar at the ovary base support the conclusions that pollinators must be relatively large and strong. An examination of inflorescences which had recently finished flowering with a total of several hundred flowers showed that fruits develop from most flowers.



14 Acanthus ilicifolius

Figure 14. *Acanthus ilicifolius* L. (from fresh material cultivated at Fairchild Tropical Garden, Miami, Florida). **A.** Spicate inflorescence (x 2/3). **B.** Flower (x 2) in longitudinal section. **C.** Flower (x 2/3) from the front. **D.** Large stamen (x 4). **E.** Small stamen (x 4). **F.** Floral diagram.

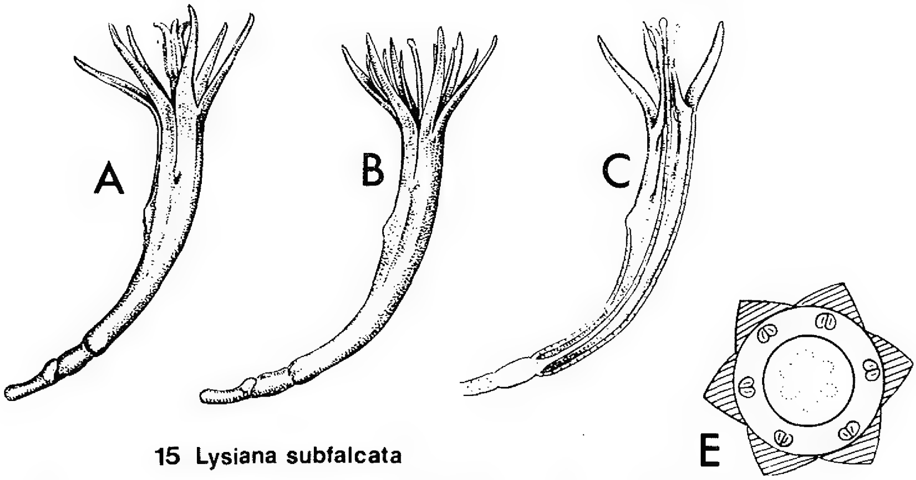
Cultivated specimens at Fairchild Tropical Garden, Miami, Florida set rather infrequent seed suggesting a degree of dependence on a fairly generalized pollinator.

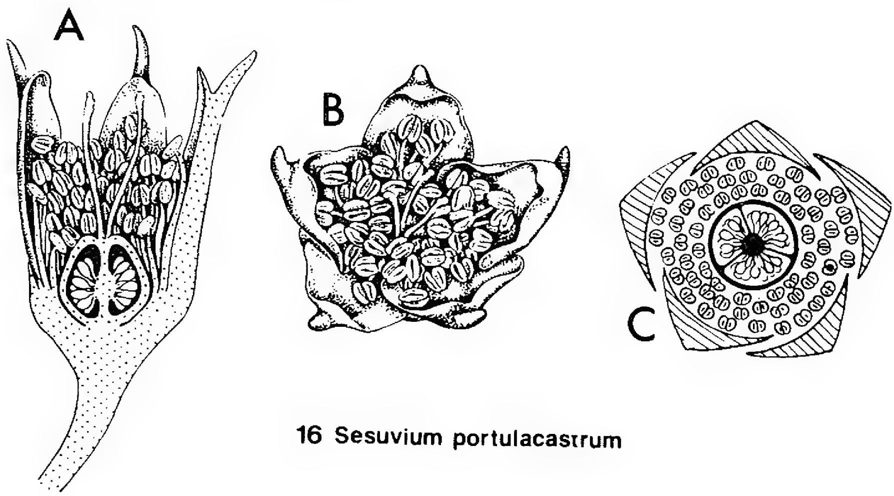
LYSIANA SUBFALCATA (HOOK.) B.A. BARLOW SPP. *MARITIMA* B.A. BARLOW (LORANTHACEAE)

This parasitic epiphyte is confined to mangrove vegetation (Barlow, 1966). The upright flowers are usually produced in two-flowered cymes. The flowers are curved back away from the branch tip (Fig. 15). The petaloid calyx tube is about 25 mm in length and 3.5 mm in width at the mouth with six flaring lobes approximately 10 mm in length (Fig. 15A, B). The inner, lower two lobes are longer than the others due to the splitting of the calyx lower down producing a slight zygomorphy. The bottom half of the calyx is red below grading into yellowish green above. The six stamens are episepalous and bear long, thin anthers covered with sticky, yellow pollen. The ovary is inferior and the stigma is ball-shaped, slightly grooved above and covered with papillae but no discernible ovules are developed, as is usual in the Loranthaceae. Since the stigma extends slightly beyond the anthers and the anthers open inward, automatic self-pollination is minimized. There is abundant pollen in the anthers of only

Figure 15. *Lysiana subfalcata* (Hook) B. A. Barlow ssp. *maritima* B. A. Barlow (from fluid-preserved material, Cape Ferguson, Townsville, Queensland). **A.** Flower (x 4/3) from the side. **B.** Flower (x 4/3) from the side with stamens removed. **C.** Flower (x 4/3) in longitudinal section. E. Floral diagram, ovary locules are stylized.

Figure 16. *Sesuvium portulacastrum* L. (from fresh material, Miami, Florida). **A.** Flower (x 4) in longitudinal section. **B.** Flower (x 4) from above. **C.** Floral diagram.





[a]indicates that the flower is fragrant [b]distance from anthers to ovary base [c]indeterminate, no ovules are produced

recently open flowers, though some pollen may also persist in older flowers. Flowers last at least three days, and often longer. The stigma becomes receptive as soon as the flower opens and remains receptive as long as the flower persists.

The flowers are visited by several species of nectar-feeding birds, principally a species of honeyeater, probably the white-throated honeyeater (*Melithreptus albogelaris*), and also the yellow-breasted sunbird and the mistletoe bird (*Dicquem hirundinaceum*). These birds fly actively between plants, probing all flowers. Many flowers have slits in the calyx tube where the birds have apparently torn the flowers to get at the nectar.

Characters of these flowers related to bird pollination are the inferior ovary for protection against the bird bill, the red calyx as an attractant, and the stickiness of pollen facilitating attachment to the bill of the bird.

Of 83 flower buds and flowers tagged, fifty-six fruit developed; fruit set was 67%.

SESUVIUM PORTULACASTRUM L. (AIZOACEAE)

This prostrate beach herb has a pan-tropical distribution. The flowers (Fig. 16) have five fleshy tepals which are pink on the inside and green on the outside. The tepals open to expose the flower parts, closing again at night and during cloudy weather, but closing finally after the flower has been pollinated. They open again at the time the capsule dehisces. There are about 25-60 stamens, 30 ovules, and 3 (−4) stigmatic lobes per flower. The stamens are pink, and mature progressively from the outside inward during the course of one day; for each stamen, first the filament elongates and then the anther dehisces. The pollen remains in the anther only a brief time as it is rapidly removed by small, pollen-collecting bees (*Trigona hockingsi* Cockerell). The stigma lobes are straight initially and gradually diverge, becoming fully spread after all the anthers have dehisced. Stigma staining shows that the receptive area of the stigma is a narrow strip on the inner surface, beginning at the tip. The stigma does not stain or stains only weakly in newly opened flowers and flowers with most of the anthers at or past dehiscence. Flowers with all the anthers past anthesis and fully divergent stigmas have deeply staining stigmas. The flowers are clearly protandrous, and stay open one to two days. Bees will occasionally probe at the stamen bases of flowers at all stages of development, however, there was no observable nectar present.

Of 29 flowers tagged, nineteen fruits developed; fruit set was 66%.

POLLEN AND OVULE PRODUCTION

The five species span a wide range in ovule production, varying from 4 to 220 ovules per flower. Flowers of *Lysiana subfalcata* do not have differentiated ovules. Pollen production per flower varies from 370 grains in *Clerodendrum inerme* to 588,000 grains in *Sonneratia alba*. Species differ in the pollen-ovule ratios, an index of the efficiency of the pollination system (Cruden, 1977). The pollen/ovule ratios are low in comparison with those calculated for several mangrove species in the Rhizophoraceae (Tomlinson *et al.,* 1978). The pollen/ovule ratio of *Clerodendrum inerme* in particular is low, suggesting that the hawkmoth pollination of this species is highly efficient. The pollen production values for *Lysiana subfalcata, Acanthus ilicifolius,* and *Sesuvium portulacastrum* are within the observed range of insect-pollinated species of the Rhizophoraceae, but considerably below the bird-pollinated species of the Rhizophoraceae. The high pollen production and pollen/ovule ratio of *Sonneratia alba* are much higher than expected for a moth-pollinated species; however, this species apparently depends on bats, birds, or wind for pollination in other parts of its range (Backer and van Steenis, 1951).

TABLE 2: Characteristics of five coastal species.

Species	Family	Habit	Typical Habitat	Distribution	Primary Pollinator	Attractant	Floral Tube length (mm)	Flower Color	Ovules Flower	Grains Flower	P/O
Sonneratia alba	Sonneratiaceae	Tree	Seaward mangroves	Old World & Australian tropics	Hawkmoths	Nectar[a]	30[b]	White	220	588,000	2673
Sesuvium portulacastrum	Aizoaceae	Fleshy herb	Sand flats	Cosmopolitan	Small bees	Pollen (nectar)	0	Pink	32	7,500	234
Clerodendrum inerme	Verbenaceae	Sprawling shrub	Beaches mangrove edges	Tropical East Australia	Hawkmoths	Nectar[a]	25	White	4	370	92
Acanthus ilicifolius	Acanthaceae	Small shrub	Landward, sub-canopy in mangroves	Tropical Australasia	Birds, Others?	Nectar	12[b]	Blue	4	4,500	1125
Lysiana subfalcata ssp. *maritima*	Loranthaceae	Parasitic shrub	Epiphyte on mangroves Trees	Tropical E. Australia	Birds	Nectar	38	Red	c	1,470	c

[a]indicates that the flower is fragrant [b]distance from anthers to ovary base [c]indeterminate, no ovules are produced

DISCUSSION

Due to the unstable nature of mangrove and beach vegetation, new areas are constantly being colonized and old habitats destroyed. Initial colonization will often be by a single seed floating in sea water. As a result, mechanisms can be expected which promote out-crossing with its associated genetic advantages, in established populations, but at the same time allow fruit set in isolated individuals. The most important such mechanism in shore line species appears to be protandry, whereby the pollen in a flower is shed before the stigma becomes receptive. Protandry promotes out-crossing by preventing individual flowers from self-pollinating, though flowers on the same plant may pollinate each other. Partial or complete protandry is found in *Sesuvium portulacastrum, Clerodendrum inerme,* and *Acanthus ilicifolius,* and in three other common mangrove trees, *Rhizophora stylosa, Bruguiera exaristata,* and *Lumnitzera racemosa* (Tomlinson *et al.,* 1978; Tomlinson *et al.,* 1979). While the sample size is not large, the presence of protandry in six out of the eight species studied indicates the importance of protandry as an out-breeding mechanism for coastal associated species.

Morphological adaptations of the flower which prevent self-pollination, generally a physical separation of the anthers and the stigma, are found in *Sonneratia alba, Acanthus ilicifolius,* and *Lysiana subfalcata.* Every one of the five species in this study has some obvious mechanism to prevent self-pollination of individual flowers though the flowers are perfect. However, fruit set is 66% or higher in plants of *Sesuvium portulacastrum, Sonneratia alba, Lysiana subfalcata,* and *Acanthus ilicifolius.* This high fruit set, despite mechanisms which prevent self-pollination in individual flowers, strongly suggests that these plants are self-compatible. Geitonogamy would allow fruit set in isolated colonizing plants. As populations increased to the high density characteristic of many mangrove species, the percentage of fruits resulting from geitonogamous pollinations would decrease as pollen was increasingly transferred between adjacent plants by the pollinators. However, the real measure of degree of out-crossing in coastal species must come from studies of the extent of self-incompatibility. In the present study, visits have been too short to permit the necessary artificial pollination, bagging, and emasculation techniques which are needed to provide unequivocal evidence for out-crossing. This research approach is the next logical step to the results presented here.

There is variation both among species and among populations within species of *Sonneratia* for the presence or absence of petals, the time of day the flowers open, and the color of the petals and stamens. These differences may be adaptations to the local pollinating fauna. Plants with red flowers which open during the day may be adapted to bird pollination, while plants with white flowers which open at night may be adapted to moth or bat pollination.

Adaptations to bird, hawkmoth, and bee pollination were evident in this group of mangrove-associated plant species. This wide range of adaptations is comparable to the divergence in flower types associated with different pollinators found within the mangrove community itself in the Rhizophoraceae (Tomlinson *et al.,* 1979) and the genus *Lumnitzera* (Tomlinson *et al.,* 1978). This research has indicated that each mangrove species shows a distinctive floral morphology and has a particular relationship to the pollinating fauna. These pollination studies only hint at the complexity of animal-plant interactions in tropical coastal communities which will be revealed by further investigation.

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